5 | The Ecology of Some Upper Palaeozoic Floras

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Abstract: The ecology of some Upper Devonian, Carboniferous and Permian floras is briefly reviewed. A number of specific examples of combined sedimentological and palaeontological studies are taken to emphasize the need for interdisciplinary analysis in fossil plant ecology. Ecological changes in the late Devonian are important with, for instance, the occurrence of trees causing a structure in plant communities not present before that time. The basic pattern in late Palaeozoic plant ecology appears to have been set late in the Devonian or early in the Carboniferous with various lowland floras being associated with specific ecological conditions. Sphenopsids and lycopods often appear to dominate lake margins and "swamp forests", whilst pteridosperms appear to dominate drier flood-plain environments. This pattern persists throughout the Carboniferous and in some regions into the earliest Permian. Upland floras are first recognized at the beginning of the Upper Carboniferous and are dominated by various gymnosperms, conifers and cordaites in particular. These floras spread into the lowland areas during the Permian. The general patterns of change in the plant ecology are thought to be controlled in part by broad climatic changes. Relationships of climate, vegetation and erosion as well as evidence for animal/plant interactions are also considered.

INTRODUCTION

This paper serves only as one to "set the scene" of the terrestrial floras during the later part of the Devonian, Carboniferous and

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Permian. I shall discuss various aspects of preservation, distribution and ecology, as well as animal/plant interactions in the broadest sense. It is not intended to be a comprehensive review of Palaeozoic plant ecology since the Carboniferous has already been adequately treated (Scott, 1977b), while for the Devonian our evidence is very incomplete. However, I hold the view of Seward (1924) who wrote: "A useful purpose will have been served if, by premature expression of opinion based on incomplete data, attention is directed to the need for fuller information and to the importance of taking stock of such knowledge as we already possess".

As few fossil plants are found *in situ*, their distribution within rock strata is controlled by transport and depositional processes. In general, fossil plant assemblages are controlled by the interactions of their original ecology with sedimentary processes. The reconstruction of original plant communities is dependent upon the understanding of transport history and depositional environments interpreted from the sedimentological evidence (Scott, 1977b). In addition not all the plants have survived the fossilization process. We probably know less than half of the plants at any one moment in time, and maybe as few as 10%. Preservational environment is as important with fossil plants as it is with vertebrates. Fossil plant material is often best preserved in acidic or anaerobic conditions, but bone is best preserved in alkaline environments (Schopf, 1975; Rayner, 1971). This fact can influence our ideas concerning the distribution of these fossils. This problem of preservational environments must, therefore, be considered in any attempt to understand terrestrial communities. Most of the famous vertebrate finds in the Carboniferous have been found in lacustrine or oxbow lake deposits (Boy, 1977). This might cause an overrepresentation of aquatic, semi-aquatic or marginal-aquatic vertebrates. Those animals living away from such environments (just as with upland floras) may not be preserved, living in erosional rather than depositional sites (Boy, 1977). In addition, vertebrates living in peat swamps, i.e. preserved in coal seams, are often found as "ghosts", the original bone not surviving the acidic conditions (Rayner, 1971).

A number of changes in the floras and plant communities from the late Devonian to the Permian may be related to climatic and evolutionary factors, and may result from the adaptation of biological strategies of the plants to these differing conditions. In this paper I shall try and trace some of these changes and try to relate them to

the evolution of tetrapods. I shall, however, restrict my comments to the "Euramerian" palaeobiological province, i.e. Europe and North America, as it is from this area that virtually all important vertebrates are found; it is also the area for which we have the fullest knowledge of late Palaeozoic ecology (Chaloner and Meyen, 1973; Panchen, 1973).

SEDIMENTARY ENVIRONMENTS

I am concerned in this paper with terrestrial vegetation, ecology and ecosystems and it is a truism to state that most of our information concerning the distribution of fossil plants comes from terrestrial sediments, although a few floras are known from near-shore marine deposits. Very often, however, either palaeobotanists are not interested in the sedimentology, or sedimentologists ignore the plants, so that our knowledge of their relationships is often scanty. As many plants live in erosional rather than depositional areas, information about the former may be difficult to obtain whereas we may tend to overemphasize the latter. Our knowledge of upland floras is scanty and until recently evidence of these floras has been generally overlooked.

The first step in reconstructing the vegetation is to observe the distribution of plant remains in various sedimentary facies. The next step involves detailed interpretation of the depositional environments and likely transport history of the plants. Only then can hypotheses be made concerning possible plant communities, which may be subsequently tested by the acquisition of new data. Such reconstructions are hazardous, but are offered in the spirit of encouraging further work and critical comment.

The Devonian continents, when reassembled to their pre-drift positions, may be shown to have spanned the Equator (Smith *et al.*, 1973), with a central "Old Red Sandstone" continent surrounded by tropical seas (House, 1968, 1974). Allen *et al.* (1967) have shown that the continental sediments were laid down under fluvial, lagoonal or lacustrine conditions. In addition they consider that equatorially there was a variable climate which was locally warm-humid. The "Old Red Sandstone" deposits may also be considered as syn- or post-orogenic and have been shown to interfinger with marine deposits (Allen *et al.*, 1967). Evidence of rainfall (its amount and variation) is difficult to assess. The common presence of concretions of caliche-

like cornstones suggest periods of low water-table (Read and Johnson, 1967). Fossil plant material in Upper Devonian strata is often found in flood-plain or near-shore marine clastic facies. Some of the characters of the Old Red Sandstone which are typical of present-day arid or semi-arid regions may have resulted from a lack of vegetation rather than a lack of rainfall (Schumm, 1968; Glennie, 1970). It is likely that a land flora first colonized near-shore or lowland alluvial areas, and this would mean that the delivery of sediment from source areas was not inhibited and sheet-like alluvial deposits could still form (Schumm, 1968). Schumm also observes that "with increased plant cover, alluvial deposits were stabilized, but large floods caused periodic flushing of sediment from the system, thereby creating cyclic sedimentary deposits".

The Carboniferous began with widespread marine transgressions which spread over the eroded remnants of the "Old Red Sandstone" continents (Ramsbottom, 1973), but it has been clearly demonstrated that this was not exactly at the Devonian/Carboniferous boundary (Sleeman, 1977; Clayton *et al.*, 1977). Consequently non-marine Lower Carboniferous rocks are of smaller extent than those of the preceding Devonian and our knowledge of the distribution of plant material in terrestrial and near-shore marine rocks is sparse. The late Carboniferous, in contrast, is characterized by large tracts of coal "swamps" spread over wide continental areas (Schopf, 1974). These coal-forming belts, which straddled the Equator (Frederiksen, 1972) belonged to a single (Euramerian) palaeobotanical province (Chaloner and Lacey, 1973). The sediments were laid down in marginal marine or alluvial swamps, on flood-plains by various types of alluvial systems, or in lakes (Wanless *et al.*, 1969; Kelling, 1974; Scott, 1978). In addition, deltaic sediments were deposited in marine or freshwater bodies. The vegetation was at least luxuriant, being responsible for forming the thick coal seams (Teichmüller, 1952, 1962), but plant material is also abundant in many of the associated sediments (Wanless, 1959; Robertson, 1952). We are able to recognize upland floras for the first time in the Upper Carboniferous (Leary, 1977), and they must have played a major role in stabilizing erosional areas just as the often dense lowland vegetation must have helped stabilize many of the alluvial systems (Robertson, 1952; Schumm, 1968).

The disappearance of the "coal swamps" at the end of the Carboniferous was probably due to a change in climate of which evidence

can be seen even in Stephanian times (Frederiksen, 1972; Phillips *et al.*, 1974). The Permian is often characterized by red beds which are generally believed to have been formed in arid or semi-arid desert conditions (Glennie, 1970; Waugh, 1973). Permian terrestrial sediments often consist of piedmont breccias, wadi-fan and dune complexes, alluvial fan and flood-plain sediments (Brookfield, 1978), deposition often taking place in a series of cuvettes which may have opened into larger basins (Laming, 1966). There is also some evidence, at least for the Lower Permian in Britain, of some moderate relief (Smith *et al.*, 1975). There appears to have only been a generally thin plant cover which declined because of diminishing rainfall.

The Upper Permian began with a widespread marine transgression (Smith *et al.*, 1975). Plant material occasionally occurs in these sediments (Stonely, 1958) and suggests a sparse conifer forest surrounding the new marine basins. These floras take on more of the character of the succeeding Mesozoic flora (Frederiksen, 1972).

CLIMATE AND WEATHER

Climatic changes and to a lesser extent weather patterns played a major role in the distribution and ecology of late Palaeozoic floras, as with those of the present day. Throughout the late Palaeozoic the Euramerian belt straddled the Equator with a slight northward drift (Smith *et al.*, 1973). The climate in Europe and North America has generally thought to have been warm, locally humid, if not hot, with red beds particularly common in the Upper Devonian (Old Red Sandstone facies) (Allen *et al.*, 1967). These continental deposits seem to show evidence of a sporadic rainfall which may be contrasted with the Carboniferous.

A more humid, but not necessarily cooler climate appears to have been extensive during the later Carboniferous and, with regular precipitation, provided an environment for luxuriant growth of vegetation and the formation of thick peat (coal) (Schopf, 1974). Evidence from sediments and from fossil charcoal suggests that, although the climate may have been fairly stable, there were variations in weather, shown by periods of drought accompanied by forest fires and by periods of storms and floods. The regular banding in some Coal Measure lacustrine deposits may suggest in addition a more regular weather cycle not recorded by woody trees in the form of growth rings (Chaloner and Creber, 1974).

At the end of the Carboniferous period, rainfall appears to have declined again. The British Permian seems to be typical of the northern continents and Smith *et al.* (1975) write that "with the decline in rainfall came a depletion of plant cover, and movement of finer sediment by prevailing easterly to east north-easterly winds became the major sedimentary process in the central areas of most depositional basins". Most of the familiar lowland habitats of the late Carboniferous seem to disappear gradually during the early Permian, so that following the mid- to late Permian transgressions those floras and faunas best adapted to drier conditions thrived when new continental areas became available.

Although it is evident that broad climatic shifts were responsible for changing sedimentological and ecological conditions, rainfall must have been a very important controlling factor. Published evidence suggests that rainfall was sporadic during late Devonian times, although it is difficult to assess the effect of no vegetation on upland areas. Vegetation was probably more uniform in the Euramerian belt during the Carboniferous, although Frederiksen (1972) suggests that "the uplands were probably cooler, less rainy, and had greater seasonal variations in rainfall than most tropical uplands do now". The increased rainfall caused swamping of lowland areas, as well as the formation of large lakes. Rainfall appears to have declined during the Permian, allowing the onset of more arid conditions. Temperatures may have remained fairly constant at the Equator at this time.

PLANT COMMUNITIES

We may consider, within the Upper Palaeozoic, two major "explosions" in land plant evolution. The first was the rise of the earliest vascular land plants and the evolution of the psilophytes in the late Silurian and early Devonian: this is, the diversification from a *Cooksonia*-type to the development of the lycopods via the zosterophylls, and the development of the trimerophytes from the rhyniophytes (Banks, 1975; Gensel, 1977). The second explosion represents the diversification of the trimerophytes and the evolution of the "pteropsids", progymnosperms and sphenopsids during the Middle and Upper Devonian (Scheckler, 1974; Gensel, 1977). By the end of the Devonian, therefore, most of the basic botanical strategies that are seen during the rest of the Palaeozoic had evolved, including gymnospermous structure, arborescent habit, true leaves and seeds (Chaloner, 1970;

Beck, 1970; Pettit, 1970; Kevan *et al.*, 1975). Further diversification and evolution was, therefore, geared to the filling of new ecological niches made available by the changing climate and sedimentary environments.

Data concerning the original ecology may be derived from the distribution of plants within sediments, the interpretation of sedimentary environments and the transport history of the plants. Alternatively, there is what may be termed the structuralist approach; that is, using the structures of the plants to deduce their ecology. This approach has been well illustrated by Weiss (1924). More recently there has been the tendency to ascribe fossil plant species to pseudoecological groupings under such terms as hygrophile biotype, mesophile biotype etc. (Remy and Remy, 1977), but perhaps this kind of compartmentalization reflects as much our uncertainty of the true ecological status of the plants rather than anything else. We are plagued by the problem of whether a plant, for instance, may have been a true xerophyte, or merely a pathological xerophyte (Wartman, 1969). Chaloner and Collinson (1975) have demonstrated that the interpretation of ecology from botanical structures can be very misleading and perhaps even dangerous. There is no doubt that the evolution of certain botanical structures may have been in response to particular environmental pressures, but it does not mean that plants possessing these structures must always be found in the same environment. The evolution of the seed may be said to enable the plant to reproduce without reliance on water being widely available, but this does not prevent the extant seed-producing conifer *Taxodium distichum* from standing with its roots and even its trunk in open water.

1. Floras of the Devonian/Carboniferous Transition

Our knowledge concerning the ecology of Upper Devonian floras is very sparse, but a few general comments may be made before taking examples from which general conclusions may be made.

Within the Euramerian area during the late Devonian there were wide continental margins (bounded to the north by shield areas) and, according to Allen *et al.* (1967) "their coastlines, complex river systems, alluvial flood plains, lagoons and lakes were ideal for the development of a wide variety of non-marine habitats for the verte-

brates". In addition this presented land plants with a diversity of niches to fill. The mid- to late Devonian diversification of land plants may have been a response to this situation.

A number of biological strategies adopted by land plants would have a direct influence on all types of animal life. The evolution of leaves (megaphylls) and the development of heterospory and the seed, for example, may relate to the evolution of herbivory in different animal groups. Perhaps the most important innovation as far as whole-ecosystem dynamics was concerned was the evolution of secondary growth which enabled plants to attain an arborescent habit. Until the early Middle Devonian most land plants were no bigger than shrubs, perhaps a metre or so high. The acquisition of secondary growth enabled some plants to increase girth, grow taller and give stability to these larger plants, now truly trees. With forests, therefore, a two-level "structure" to the ecology can be discerned for the first time: a division into a tree-top ecosystem and a ground-cover ecosystem (see Gosz *et al.*, 1978). It has been argued that this acquisition of an arborescent habit by plants stimulated the evolution of flying arthropods (Kevan *et al.*, 1975). Theoretically this structuring of plant communities would have given great stimulus to both animal and plant evolution, providing a wide range of new ecological niches to be filled.

Most known Upper Devonian floras come from continental or near-shore marine deposits. In the British Isles our only well-known flora comes from the Devonian/Carboniferous boundary at Kiltorcan, County Kilkenny, Ireland. More diverse and widespread floras are known from North America and it is these that I shall describe first.

The sediments of the Middle and Upper Devonian of the Appalachian region, including New York, are rather similar to the British Old Red Sandstone. These continental rocks, known as the Catskill facies, interfinger westwards with marine rocks (Allen and Friend, 1968). According to these authors, commenting on the similarity of some European and American facies: "Assuming continental drift, a rational Devonian palaeogeography is developed for the North Atlantic region that involves the symmetrical occurrence of marine influenced coastal plains in relation to the unified Caledonide fold belt, a number of intermontane basins apparently unconnected with the sea". These authors have shown that sediments of braided streams (Pocono facies), meandering streams and tidal flats (Catskill facies) and coastal barrier and shelf (Chemung facies) may be encountered.

Banks (1966) has described the stratigraphic distribution of the Middle and Upper Devonian floras of New York State. A few comments concerning the sedimentological distribution of some of these Upper Devonian floras may be made. Banks' list gives a good indication of those plants occurring together at one locality. *Archaeopteris* is abundant in the Oneonta Formation in the Catskill facies and is associated with *Tetraxylopteris, Aneurophyton, Schizopodium, Drepanophycus* sp. and *Colodexylon* sp. (At other localities *Callixylon* spp., the wood of *Archaeopteris*, are also present.) Slightly higher in the succession in the Walton Formation, in the same facies, a number of species of *Archaeopteris* plus *Callixylon* are present. In the Chemung facies, *Taenocradia, Knorria* and *Lepidosigillaria* are present. Within the Catskills there is also some ecological diversity illustrated by the palynomorphs, with *Geminospora* dominating spore assemblages of the tidal Catskill facies, together with other plants, fish and the bivalve *Archanodon*, while *Ancyrospora* dominates sediments of the flood-plain (Catskill, interior facies) associated with fish and plants (Berg, 1977; J. Richardson, personal communication).

Similar palynological results have been obtained from Belgium where hystrichospores (e.g. *Ancyrospora*) are abundant in coarse sediments and are presumed to "originate with fluvial sediments from 'uplands'" (Streel, in Becker *et al.*, 1974). Where the sediments are fine, however, the spore flora is dominated by *Aneurospora greggsii* which possibly represents the local (*Archaeopteris*?) Frasnian vegetation (Streel, ibid.).

Beck (1964) has already commented on the predominance of *Archaeopteris* in the Upper Devonian flora of the Western Catskills, in the near-shore or tidal facies. From its abundance and good preservation and rarity of other species, Beck concludes that the coast of this "Upper Devonian inland sea, in the region studied, was probably densely forested by woody plants of which *Archaeopteris* was the most common".

Evidence from British Old Red Sandstone deposits is very sparse. Most of the Upper Devonian rocks consist of red sandstones and conglomerates, and these facies persist in many areas until well into the Tournaisian (Carboniferous). The one area from which we have any detailed knowledge of the stratigraphy, sedimentology and flora is in County Kilkenny, south-eastern Ireland. The flora from this region has long been realized to be of importance (Haughton, 1855). This flora is best known from the Kiltorcan Formation, approxi-

mately equivalent to the "Yellow Sandstone Series" of the old surveyors (Holland, 1977). The flora and fauna are best known from the type locality on Kiltorcan Hill and are less evident elsewhere (Holland, 1977; Colthurst, 1978). The classic old quarry, from which most of the famous Kiltorcan flora was obtained, has yielded almost exclusively an assemblage of the progymnosperm *Archaeopteris* and the lycopod *Cyclostigma* (Chaloner, 1968). In addition, however, specimens of the seed *Spermolithus devonicus* have been recorded during the recent excavations by W. G. Chaloner (Chaloner *et al.*, 1977). Rarer specimens of *Ginkgophyllum kiltorkense* and *Sphenopteris hookeri* have also been recorded (Johnson, 1914).

A new quarry at Kiltorcan Hill exposes fossiliferous strata approximately 3 m above the level in the "classic" quarry (Colthurst, 1978). Recent collecting by Chaloner and the author has yielded abundant *Lepidodendroposis*, leaf fragments cf. *Rhacopteris* and seeds very similar to *Spermolithus devonicus*. Both of these assemblages are presently being studied by W. G. Chaloner and W. S. Lacey. These floras are from approximately the Devonian/Carboniferous boundary, and Chaloner (see Holland, 1977) has commented on the close similarity of the lower assemblage to the *Cyclostigma/Archaeopteris* flora from Bear Island (Kaiser, 1970) which has an associated spore flora of Tournaisian (Tn1a) age (= PL Zone; K. Higgs, personal communication). Recent palynological work in the Kiltorcan area has shown that rocks a little way above the plant-bearing horizons are of Tournaisian (Tn1b–Tn2) age, (VI zone; Clayton *et al.*, 1977). New unpublished data show that rocks stratigraphically below this horizon elsewhere yield a PL Zone spore assemblage (K. Higgs, personal communication), the position of the PL/VI boundary not being known.

The sediments in the "classic" quarry consist of fine greenish-yellow sandstones and siltstones overlying coarse flaggy cross-bedded sandstone (Colthurst, 1978). The plant material consists either of branches of *Archaeopteris*, occasionally fertile, or stem fragments (leaves and sporophylls) of *Cyclostigma*. These are preserved in a chloritoid which is replacing a coalified compression (Chaloner, 1968; Schopf, 1975). Colthurst (1978) has interpreted these sediments as representing a bar-tail in a meandering channel. In addition to the flora an interesting fauna has been recorded, consisting of the bivalve *Archanodon jukesii,* fish including *Coccosteus* and crustaceans

(Forbes , 1853; Harper, in Gill, 1956). No bivalves or fish, however, were found in the most recent excavations of the classic quarry. The plants occur in fairly coarse silts and sands as well as in finer silts. Although often occurring together, *Archaeopteris* is more often found in coarser sediment than *Cyclostigma*. It is interesting to note that no pieces of *Archaeopteris* trunk, known as *Callixylon*, have been recorded.

The plant material in the newer, or council, quarry is found near the top of the section in laminated sandy silts which overlie green-, brown- and red-coloured mudstones. The plants, according to Colthurst (1978), occur in finer grained laminae within the more silty units. Colthurst interprets these sediments as being deposited during flash floods in small, shallow ephemeral lakes or on near-coastal flood-plains.

The main problem concerning these two floras is to know whether they are more or less contemporaneous and whether their distribution is ecological rather than stratigraphic. The fauna may have been washed into a small abandoned meander of only local occurrence. Berg (1977) has shown that American species of *Archanodon* may have lived in flowing rivers and were in fact burrowers. No burrows have been recorded from Kiltorcan. With such little data the reconstruction of the plant ecology is difficult.

The Kiltorcan beds span at least two spore zones (PL and VI) and rocks of similar age are present in England in the Avon Gorge. Utting and Neves (1970) record a lower assemblage of spores, within the Old Red Sandstone, which may be placed in the PL Zone (K. Higgs, personal communication). The transition beds to the Lower Limestone Shales yield a macroflora containing abundant *Rhacophyton*. VI Zone spores are recorded from a sample above this horizon within the lowest part of the Lower Limestone Shales. The macroflora may be considered as possibly being of a similar age to the Kiltorcan flora and the distribution of these genera may be ecological rather than stratigraphic. Three separate plant assemblages occur in the uppermost Devonian/Lower Carboniferous rocks: an *Archaeopteris/Cyclostigma* assemblage; a *Lepidodendropsis* assemblage; and a *Rhacophyton* assemblage. All three are world-wide in distribution (Zalessky, 1931; Iurina and Lemoigne, 1975; Andrews and Phillips, 1968; Nathorst, 1902), with the *Lepidodendropsis* assemblage dominating Lower Carboniferous floras world-wide (Chaloner and Lacey, 1973).

2. Lower Carboniferous Floras

As with the previous floras, we have little data on those of the lowest Carboniferous (Tournaisian). Most of these floras have been recovered from either Old Red Sandstone facies (Matten *et al.*, 1975) or from marine rocks (Hoskins and Cross, 1941). Some of the well-known Tournaisian floras (e.g. Barnard and Long, 1973) now appear to be Lower Viséan in age (Scott, in preparation). In Britain we have a number of important Viséan compression and petrified floras from near-shore marine and non-marine sequences. When, however, floral lists are compared, few species are found in common. Most of the detailed work has been done on the petrified floras and, although our knowledge of the stratigraphic distribution of compression floras is great (Crookall, 1932), we have little knowledge of their ecological distribution. This being so I will briefly mention two localities which I am at present studying.

One of the best known Lower Carboniferous floras is that of the Loch Humphrey Burn, north of Glasgow, studied by J. Walton and his student D. L. Smith (e.g. Walton *et al.*, 1938; Smith, 1964). These authors described a wide range of plants preserved both as petrifactions and as compressions. Recent field investigation has shown that there is more than one plant bed. The lowest part of the section consists of green silts with upright *Archaeocalamites*. Its cone *Pothocites* is also present. This bed is overlain by a fusain-rich drifted coal followed by yellow–green siltstones and mudstones containing a pteridosperm-rich flora. Siltstone blocks at the base of this bed contain contorted fronds of *Rhacopteris* and *Spathulopteris*. The sediments, which have been dated palynologically as Lower Viséan in age (G. Clayton, personal communication), may be interpreted as marginal-lake and alluvial flood-plain sediments and have some analogy, both sedimentologically and palaeoecologically, with some Coal Measure sediments (Scott, 1978). The *in situ Archaeocalamites* may have an analogy with the marginal-lake reed-swamp *Calamites* of the later Westphalian. The upper part of the sequence may represent flood-plain and river deposits, the siltstone blocks being reworked channel bank collapse deposits (Scott, 1978) which may have incorporated plants living on the river banks. Not surprisingly these data give us a picture of the rich pteridosperm flora being associated with the river banks and flood-plain. Smith (1964) con-

sidered that the flora from Glenarbuck, nearby, which consisted mainly of lycopods, may be of the same age but represented a different ecological situation. As yet, however, there are no data as to the precise age of this deposit so no further comment can be made.

The second example is from Lower Carboniferous sediments (Lower Viséan: Chadian) of north-west Ireland. Here, in near-shore marine deposits (Shalwy beds) of the Donegal Syncline (George and Oswald, 1957), there are a number of fusain bands. The bands, up to 50 in all, occur in carbonate-rich sandstones which also contain a shallow marine fauna—gastropods, ostracods, brachiopods, foraminifera, nautiloids and fish teeth—and a flora of algae. The fusain bands contain an almost monotypic flora or a herbaceous lycopod which is extremely well preserved and has been studied using SEM (Scott and Collinson, 1978). Although other plants are present they are rare in comparison with the lycopod. As yet this plant has not been identified, but is still under study. The rock is black with the fusain which consists of 1–3 cm long stelar fragments and 1 cm cubes and irregular fragments of other tissues. The occurrence of such fusain in thick (up to 1 cm) numerous bands in near-shore marine deposits may be the result of storms washing in debris from coastal areas following extensive forest fires over a lycopod scrubland. This deposit, together with a similar deposit from County Mayo, is still being studied and further results may help in interpretation.

Daber (1959, 1964) recognized in Middle Viséan rocks of Germany four plant associations: *Asterocalamites* association; *Sphenophyllum* association; a lycopod coal seam association; and a general pteridosperm assemblage.

Finally, there is the Upper Viséan Pettycur flora from Scotland. This flora was first described as a whole by Gordon (1909). The flora, although dominated by ferns and pteridosperms, also contains lycopods and sphenopsids. Further investigation of the sedimentology and field relations of this deposit may give some idea of the palaeoecology of this interesting flora.

3. Upper Carboniferous Floras

As with the Upper Devonian and Lower Carboniferous, our knowledge of the ecology of early Upper Carboniferous floras (Namurian)

is incomplete. We have some idea of the range of plants present from well-known compression floras, but know little of their structure, except in a few isolated cases (Hass, 1975).

Recent work by Leary (1974, 1975, 1977) and Leary and Pfefferkorn (1977) has for the first time given us a detailed picture of Namurian upland, lowland and mixed plant assemblages (see also Havlena, 1961). Both of the floras described by Leary contain the enigmatic plants *Megalopteris, Lesleya* and *Lacoea*, and have high percentages of pteridosperms and Noeggerathiales, and a low percentage of ferns and lycopods which contrasts with their dominance in lowland or swamp communities. There can be little doubt that these plants were associated with upland environments. This work by Leary and others is of special importance as it gives us, for the first time, a chance to separate two distinctive floras (upland and lowland/swamp) which can be seen in the succeeding stages, and an assessment can be made concerning the evolutionary diversification of floras in both. It is often considered that the climatic change at the end of the Carboniferous enabled upland floras to spread into the lowland basins (Frederiksen, 1972), thus proving a very different setting for later tetrapod evolution. In addition, upland plant cover may have had a major role in stabilizing erosional areas (Schumm, 1968).

As has been previously mentioned, the distribution of floras is controlled sedimentologically as well as ecologically. I have shown that in the Westphalian of Britain lacustrine sequences yield a sparse flora which is species-poor but which often yields an abundant and sometimes diverse fauna. Many of the best Namurian vertebrate localities occur in sequences which are dominantly lacustrine, often associated with fish and non-marine bivalves (Andrews *et al.*, 1977). Plants are rarely recorded in such sediments. It is often difficult, therefore, to assess vertebrate/plant interactions (but see below).

By early Westphalian times a variety of upland and lowland plant associations were well developed. Evidence for this may be derived from macro- as well as from microfloral data (Sabry and Neves, 1971; Scott, 1977b). Sabry and Neves (1971) concluded from palynological evidence that two principle plant associations were established at this time in southern Scotland, namely a lycopod–*Calamites* swamp flora and a *Cordaites*–conifer backswamp and/or upland flora. It is interesting to note that from the same area (Sanquhar Coalfield) evidence suggests that the upland flora disappeared later in the Westphalian

because of an overstepping and possible erosion of the upland area (Scott, 1976).

The ecology of Westphalian floras has been well documented and I will only summarize the main results here (for fuller reviews see Havlena, 1971; Scott, 1977b). Most recent work on coal-ball floras suggests that coals, particularly in the Pennsylvanian of North America, are dominated (in terms of biomass) by arborescent lycopods, but occasionally by other plants (Darrah, 1941; Phillips *et al.*, 1977). These floras have also been shown to change through time to become dominated by large tree ferns such as *Psaronius*, probably as a result of "broad climatic shifts" at the close of the Carboniferous (Phillips *et al.*, 1974).

Peppers and Pfefferkorn (1970), working with data from compression floras and palynology, recognized a variety of lowland associations: a wet swampy association with lycopods, ferns and rare *Cordaites*; dry swampy with ferns, lycopods and sphenopsids; levees and flood-plains with pteridosperms, ferns and sphenopsids; and upland with pteriodsperms, *Cordaites* and rare Noeggerathiales. European workers have basically come to similar conclusions (Daber, 1964; Oshurkova, 1967; Havlena, 1971).

Recent work on Westphalian floras in Britain has suggested that the peat- (coal-) forming vegetation, or "swamp", was dominated by various groups of lycopods; the flood-plain areas supported a flora dominated by pteridosperms with some ferns, sphenopsids and lycopods; levee banks of meandering rivers supported various pteridosperms; whilst *Calamites* grew around the lakes and on point bars (Scott, 1978, 1979). It has also been suggested that the upland supported a cordaite–conifer forest (Chaloner, 1958).

Evidence from America indicates an extensive uppermost Carboniferous upland flora dominated by *Taeniopteris, Walchia* and *Dichophyllum* (Cridland and Morris, 1963).

4. *Permian Floras*

Most of our knowledge of the ecology of Permian floras comes from the work of German authors (Gothan and Gimm, 1930; Gothan and Remy, 1957; Barthel, 1976) on floras from the Rotliegende (Lower Permian). Gothan and Gimm (1930) investigated the distribution of plants occurring in different rock types from a number of sections

in Thuringia. These authors (and later Gothan and Remy, 1957) recognized two main plant assemblages: a *Pecopteris-Calamites* assemblage associated with lowland and coal-forming environments, and a *Callipteris-Walchia* assemblage associated with an upland environment. This was one of the first papers to detail upland floras in the Palaeozoic, although their presence has been suspected from the time of Witham (1833).

Barthel (1976), in an extensive monograph on the Rotliegende flora from Saxony, considered that five plant communities could be recognized:

(1) A hygrophile community with *Cordaites, Psaronius, Eucalamites*, and sphenopterids, locally with *Nemejcopteris feminaeformis* which lived in swamp (coal-forming) forests.
(2) A hygrophile community with *Stylocalamites gigas* (sporadically with other *Calamites*) in pure lake-side stands.
(3) A hygrophile community with *Nemejcopteris feminaeformis* and *Sphenophyllum oblongifolium* (sporadically with *Botryopteris burgkensis, Taeniopteris jejunata, Eucalamites*) in large stands, but not coal-forming, forming a reed-swamp surrounding short-lived lakes.
(4) A species-rich mesophile pteridosperm community (with other gymnosperms, sporadically with ferns) accumulated in rivers or remote lakes and on sandbanks within swamps.
(5) A xerophitic community with conifers, poacordaites and other gymnosperms in erosional areas with remote underground water.

Frederiksen (1972) has pointed out that during the early Permian plants were already migrating from the uplands down into the basins. This migration was a result of a climatic change which caused the diverse swamp and lowland habitats to disappear to be replaced by drier habitats. This major climatic change, which has already been discussed, caused the extinction of many of the familiar Upper Carboniferous plants such as the arborescent lycopods (Chaloner, 1967).

Later Permian floras (and subsequent Mesozoic floras) were dominated by gymnosperms (Stoneley, 1958; Frederiksen, 1972). It is interesting to note finally that the late Palaeozoic was a time for the palaeogeographic diversification of floras (Chaloner and Meyen, 1973).

ANIMAL/PLANT INTERRELATIONSHIPS

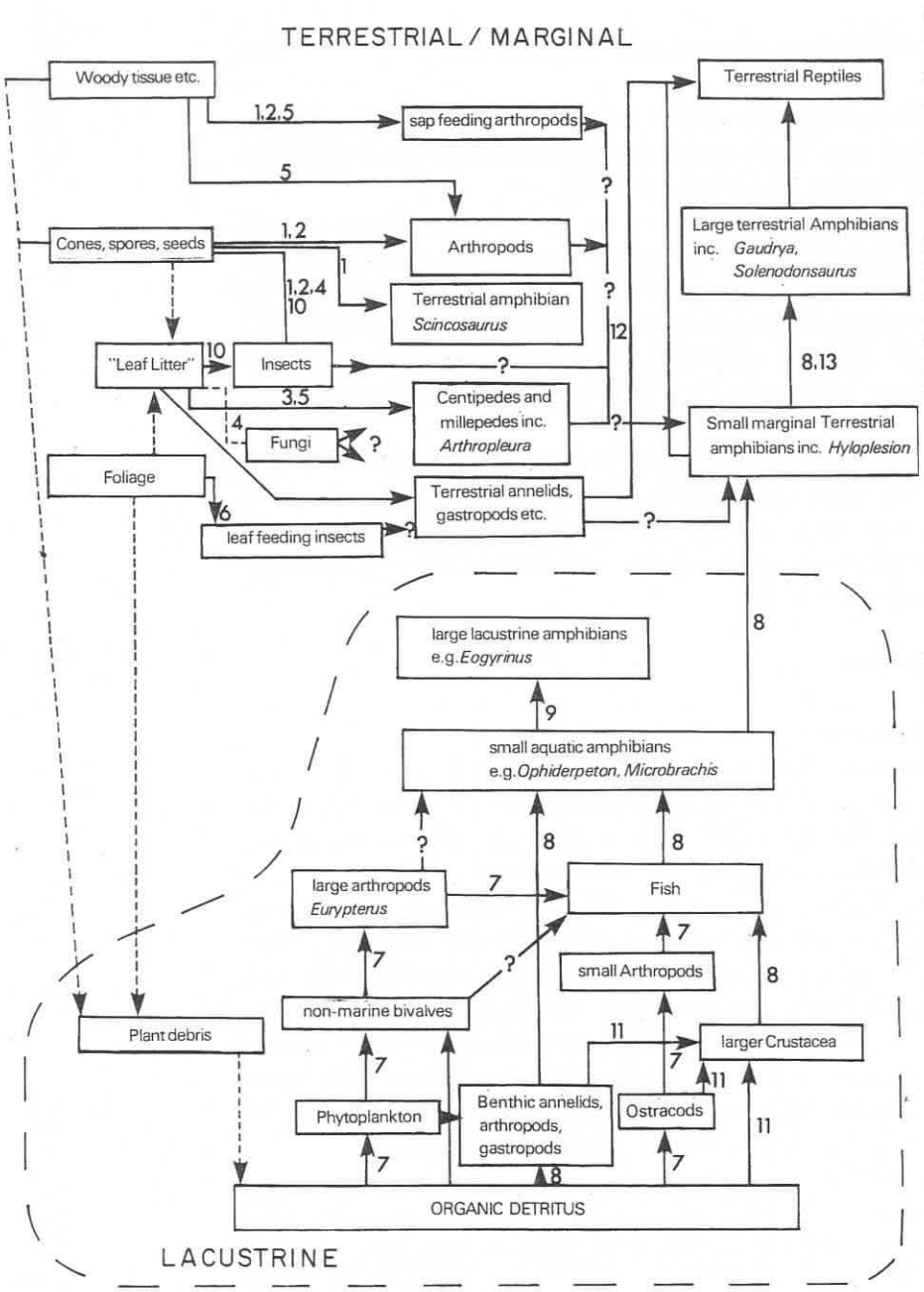
Kevan *et al.* (1975) have shown how, from the early Devonian, there were close relationships between arthropods, vascular plants and fungi. There is no doubt that these interrelationships continued and indeed diversified during the later part of the Palaeozoic. These authors have also pointed out that arborescence and structures on the stems of plants preceded flying insects and may have acted as an evolutionary stimulus. The evolution of trees, as already mentioned, must have caused some structuring of ecosystems not seen before that time, i.e. into an upperstorey, or tree-top, ecosystem and an understorey ecosystem, the one affecting the other. One of the results may have been the shading of the undergrowth and the development of microclimates which may have stimulated the evolution of tetrapods adapted to such new ecological niches.

In general two major, but related, ecosystems may be considered; the lacustrine and the terrestrial systems (Fig. 1).

1. Lacustrine Systems

These, being the sites for sediment deposition, are often those from which most data concerning faunal associations may be obtained. Commonly, most lacustrine deposits in the Coal Measures yield non-marine bivalves and, in addition, ostracods and fish (Pollard, 1973; Bless and Pollard, 1973). Less frequently, but perhaps more importantly, these deposits yield vertebrate faunas often rich in species (Milner and Panchen arity of such faunas must reflect, as Rayner (1971) has pointed out, unfavourable conditions of preservation rather than their absence from the system (Boy, 1977). A. R. Milner (Chapter 17 of this volume), in particular, has shown how data from assemblages of vertebrates may be used to build up a reasonable picture of the food web.

Most of the amphibians are thought to have been carnivorous, feeding on smaller vertebrates or arthropods. Fish probably fed on non-marine bivalves, ostracods, other arthropods and other invertebrates. These other animals probably fed either on each other or on the accumulation of organic detritus, which consisted of vascular plant material washed into the system, algae or decaying animal material (Bless and Pollard, 1973; Moore, 1968; Schram, 1976). Gensel and Skog (1977) have recently commented: "Also it is


TERRESTRIAL / MARGINAL
Woody tissue etc.
1.2.5
sap feeding arthropods
Terrestrial Reptiles
5
?
Cones, spores, seeds
1.2
Arthropods
Large terrestrial Amphibians inc. Gaudrya, Solenodonsaurus
1
1.2.4 10
Terrestrial amphibian Scincosaurus
?
12
"Leaf Litter"
10
Insects
?
8.13
3.5
Centipedes and millepedes inc. Arthropleura
4
Fungi
?
?
Small marginal Terrestrial amphibians inc. Hyloplesion
Foliage
Terrestrial annelids, gastropods etc.
6
leaf feeding insects
?
?
large lacustrine amphibians e.g. Eogyrinus
8
9
small aquatic amphibians e.g. Ophiderpeton, Microbrachis
?
8
8
large arthropods Eurypterus
7
Fish
7
7
?
small Arthropods
8
non-marine bivalves
Plant debris
11
larger Crustacea
7
7
11
7
Phytoplankton
Benthic annelids, arthropods, gastropods
Ostracods
11
7
8
7
ORGANIC DETRITUS
LACUSTRINE

quite possible that tetrapods or crossopterygians of the Mississippian swamps snatched the seeds from the water surface as a potential food source and further dispersed the seeds . . .".

Vascular plants may be considered as sedimentary filters as well as being the source of organic detritus. I have suggested that through the late Palaeozoic the Coal Measure lakes were surrounded either by large lycopod swamp forests or else by "reed-swamps" formed by large sphenopsids such as *Calamites*. These may have been used by some of the larger vertebrates as "hideouts" from which to ambush their prey!

It is interesting to note that it is this environment which persists unchanged in its basic ecological structure throughout the later Carboniferous and into the Lower Permian, perhaps accounting for the conservatism in many of the vertebrate faunas of this age (Milner and Panchen, 1973).

2. Terrestrial Systems

Data on true terrestrial systems is somewhat sparser. As has been discussed earlier we have been able to build up a fairly detailed vegetational picture, but data on the faunas and their relationship to the floras are lacking. Good terrestrial faunas, both of vertebrates and arthropods, are sparse, and data have been obtained from only a few localities. I have discussed elsewhere data concerning plants as food (Scott, 1977a). Most workers seem to agree that the majority of late Palaeozoic vertebrates were carnivorous, feeding on smaller vertebrates and arthropods, especially insects (Olson, 1976). Olson also considers that late in the early Permian "coincident with the co-evolution of reptiles and insects, however, semi-aquatic reptilian herbivores emerged (best known being *Edaphosaurus*) presumably feeding on the vegetation in and around freshwater lakes and streams".

Fig. 1. A simplified hypothetical Coal Measures food web. Solid arrows show the direction of energy flow, dashed arrows indicate decay products. Data from: (1) Scott, 1977a; (2) Smart and Hughes, 1973; (3) Rolfe and Ingham, 1967; (4) Kevan *et al.*, 1975; (5) Hoffman, 1969; (6) Van Amerom, 1966; (7) Bless and Pollard, 1973; (8) Milner, Chapter 17 of this volume and personal communication; (9) Panchen, 1970; (10) North, 1931; (11) Schram, 1976; (12) Dawson, 1860; (13) Carroll, 1967.

It is interesting to note that this emergence of reptilian herbivores occurs in the early Permian when there is a marked change in Euramerian floras probably caused by a change in climate. There would also have been an environmental crisis with many of the vertebrate inhabitants vanishing. This crisis may have stimulated the evolution of new types, mainly reptiles which could exploit the new environments including using the vegetation as food—a strategy not tried to any great extent previously. Panchen (1973) has pointed out, however, that *Edaphosaurus* appears in the late Carboniferous and is likely to have herbivorous forebears. Other tetrapods such as *Diadectes* may have been herbivorous so that the picture of the change in floras stimulating herbivory in tetrapods may not be completely accurate.

The luxuriant vegetation of the Carboniferous, little exploited by the vertebrates as food, would have provided a variety of arthropods with a range of diet. Published evidence suggests litter feeders, sap feeders, and cone- and seed-feeding insects, myriapods and other arthropods (Smart and Hughes, 1973; Scott, 1977a). Finds of insects and other terrestrial arthropods in the Coal Measures are as infrequent as those of tetrapods, the two rarely occurring together or with plants, probably because each has different preservational requirements (Rayner, 1971; Olson, 1976; Boy, 1977). Many of the well-known insect faunas have, however, been recorded from outside the Euramerian area (Riek, 1970, 1973).

One of the most interesting sites which yields data for the understanding of terrestrial faunas and floras must still be that of Joggins, Nova Scotia. Here, in mid-Westphalian rocks, a rich fauna is preserved inside hollow trunks of trees (Dawson, 1860; Carroll, 1967). The trunks of the trees were apparently hollow, caused by the centres of the stumps rotting away (Carroll, 1967). These hollow stumps served as traps for animals living on the land surface and Carroll (1967) considers that they survived for some time within the trees as there is a considerable amount of coprolitic material associated. A diverse vertebrate fauna (reptiles and amphibians) as well as invertebrates (myriapods, terrestrial gastropods etc.) are preserved (Dawson, 1860; Carroll, 1967). Dawson (1860) records fossil charcoal from the base of some of the Joggins trees and it may well be that some of these lycopods in fact represent burnt-out stumps following forest fires (Scott and Collinson, 1978). It is clear that this deposit gives us the most complete picture of a terrestrial fauna and illustrates the general

problem of inadequate data from other sites because of the nature of the preservational environment.

The interactions of plants and tetrapods, therefore, would appear to be less of one of diet rather than one of shelter and protection. Likewise with the insects, although more are thought to be herbivorous (phytophagous); North (1931) has commented that

> We have still less to go upon in connection with the feeding habits of the flying insects, but such evidence as is available concerning their mouthparts, and comparison with their nearest living representatives suggest that many of them were carnivorous. They probably preyed upon the blattoids and it has been suggested that the similarity of the blattoid wing and a pinnule of *Neuropteris* may have afforded some measure of protection to the insect, and if that is the case it is a very early instance of mimicry.

CONCLUSIONS

Our knowledge concerning the ecology of late Palaeozoic floras, in particular, of the Euramerian area, has increased rapidly over the last decade. Work in both Europe and North America has indicated that a wide variety of "plant communities" flourished, each under different ecological conditions. These may be divided into three main groups: the floras of the lowland swamps; the floras of the drier lowland environments; and upland floras. Importance must be placed on the close integration of sedimentological and palaeontolocigal studies.

Most of the biological strategies adopted by vascular land plants in the late Palaeozoic had evolved by the end of the Devonian. Two of these, arborescence and the production of seeds, must have had a dramatic effect on the evolving ecosystems, enabling plants to spread into new ecological niches as well as causing a two-level community structure in forest ecosystems which may have had a profound influence on tetrapod evolution. Although data are sparse, evidence suggests that the basic ecological associations of plants adopted in the early Carboniferous continued with some evolution and diversification throughout the rest of the Carboniferous and into the early Permian. In particular, there appears to have been a greater diversification in the presumed upland floras. The spread of these floras may have caused the stabilization of erosional areas and affected the patterns of sedimentation (Table I). Floras of the lowlands and the coal swamps in particular appear to have been more conservative.

Table I. Some factors affecting Upper Palaeozoic ecosystems

ECO-LOGICAL FACTOR / AGE	EARLY DEVONIAN	LATE DEVONIAN	EARLY CARBONIFEROUS	LATE CARBONIFEROUS	EARLY PERMIAN
PLANT COVER	Small herbaceous plants in lowland alluvial floodplain and coastal areas but mainly near water.	Herbaceous plants, shrubs and trees living in lowland areas. Coastal forests.	Diverse lowland plant communities including forests.	Extensive plant cover of both lowland and upland areas with diversification of floral communities.	Demise of lowland swamp environments with extinction of some plant groups. Upland floras spread into lowland and coastal areas.
CLIMATE AND INFLUENCE OF WEATHER	Warm - humid plant growth restricted to areas with good water supply.	Warm - humid. Two level forest ecosystem gives rise to forest micro-climate. Difficulty in interpreting climatic regime because of lack of plant cover on upland areas.	Warm - humid with wet periods and peat formation. During dry periods lightning strikes cause extensive shrub fires.	Generally wet-humid with extensive peat formation but also dry periods with frequent forest fires.	More arid climate with swamp areas drying out.
ANIMALS	Fish confined to channel systems, land arthropods.	Diversification of terrestrial arthropods and possibly evolution of flying insects.	Arthropods dominate land fauna. Early amphibians.	Arthropods including insects dominate the land fauna but amphibians an important element.	Amphibians, reptiles and mammal-like reptiles all important elements of the land fauna.
SED-IMENTOLOGY	Channel stabilisation. Total run-off in upland areas.	Increased floodplain and channel stabilisation but still upland run-off.	Generally stable lowland areas but forest fire causes increased erosion.	Stabilisation of upland areas in part by plants. Influence of plants upon sedimentation.	Climate causes depletion in plant cover, increased erosion and wind blown sediments.
OTHER COMMENTS	Problem of facies identification. Earliest evidence of animal/plant interactions.	Delay factor - i.e. in the evolution of trees and the occurrence of flying insects.	Problems of stratigraphic correlation and facies identification.	Diversification of plant communities may have stimulated the evolution of vertebrates to inhabit new ecological niches.	The major climatic change enable plants well adapted to the new conditions to survive and hence diversify.

Changes that did occur were probably due to broad climatic changes at the end of the Carboniferous and in the Permian. By the mid-Permian most of the lowland swamp areas had dried out allowing the spread of typical upland floras dominated by conifers to spread down into the arid lowland basins. This change in the distribution of the floras and their ecological setting would have had a marked effect on the various groups of tetrapods present in these different environments.

The vegetation of the late Palaeozoic may not have been a major food source for the vertebrates, but rather provided shelter and protection. This apparently changed with the ecological crisis in the Permian.

Finally, it may be reiterated that any attempt at ecosystem analysis is extremely hazardous, but I hope that this review may stimulate further investigations.

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